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Assessing landscape structure and pattern fragmentation in semiarid ecosystems using patch-size distributions

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Abstract. Spatial vegetation patterns are recognized as sources of valuable information that can be used to infer the state and functionality of semiarid ecosystems, particularly in the context of both climate and land use change. Recent studies have suggested that the patch-size distribution of vegetation in drylands can be described using power-law metrics, and that these scale-free distributions deviate from power-law linearity with characteristic scale lengths under the effects of increasing aridity or human disturbance, providing an early sign of desertification. These findings have been questioned by several modeling approaches, which have identified the presence of characteristic scale lengths on the patch-size distribution of semiarid periodic landscapes. We analyze the relationship between fragmentation of vegetation patterns and their patch-size distributions in semiarid landscapes showing different degree of periodicity (i.e., banding). Our assessment is based on the study of vegetation patterns derived from remote sensing in a series of semiarid Australian Mulga shrublands subjected to different disturbance levels. We use the patch-size probability density and cumulative probability distribution functions from both nondirectional and downslope analyses of the vegetation patterns. Our results indicate that the shape of the patch-size distribution of vegetation changes with the methodology of analysis applied and specific landscape traits, breaking the universal applicability of the power-law metrics. Characteristic scale lengths are detected in (quasi) periodic banded ecosystems when the methodology of analysis accounts for critical landscape anisotropies, using downslope transects in the direction of flow paths. In addition, a common signal of fragmentation is observed: the largest vegetation patches become increasingly less abundant under the effects of disturbance. This effect also explains deviations from power-law behavior in disturbed vegetation which originally showed scale-free patterns. Overall, our results emphasize the complexity of structure assessment in dryland ecosystems, while recognizing the usefulness of the patch-size distribution of vegetation for monitoring semiarid ecosystems, especially through the cumulative probability distributions, which showed high sensitivity to fragmentation of the vegetation patterns. We suggest that preserving large vegetation patches is a critical task for the maintenance of the ecosystem structure and functionality.

Key words: Acacia aneura; *Australia; banded landscapes; desertification; disturbance; drylands; Mulga; patch-size distributions; pattern fragmentation; periodicity; power law; vegetation patterns.*

Introduction

The effects of climate change and the massive anthropogenic alteration of natural habitats are considered the main threats to global biodiversity (Sanderson et al. 2002, Jackson and Hobbs 2009). These impacts are particularly dramatic in drylands (~30% of the Earth's land surface) where landscapes are especially sensitive to degradation (i.e., the loss of ecosystem functionality) and where restoration efforts face important constraints (Suding et al. 2004). Monitoring the integrity of the fundamental properties that regulate ecosystem function is critical in order to maintain the stability of water-limited landscapes (Tongway and Ludwig 2011).

The vegetation of many of the world's water-limited ecosystems shows distinct spatial patterns structured as a mosaic of densely vegetated patches interspersed within a bare soil background (Deblauwe et al. 2008). In the last decade, both theoretical and empirical studies have focused on the analysis of the origin, functioning, and maintenance of these patterned ecosystems (Klausmeier 1999, Tongway and Ludwig 2001, Saco et al. 2007). A critical finding from these studies has been that patchy ecosystems frequently show dynamic nonlinear behavior, and therefore, sudden catastrophic shifts from patterned to bare homogeneous or "desert" landscape states may occur in response to external stresses (Rietkerk et al. 2004). The analysis of observed spatial patterns is gaining increased attention as a

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practical way to infer the state and functionality of these systems (Sole 2007, Thompson et al. 2008, Kefi et al. 2011). In fact, landscape degradation is typically reflected in the spatial organization of dryland vegetation through the loss of patchiness or pattern fragmentation (Valentin et al. 1999, Wu et al. 2000, Wilcox et al. 2003).

Recent studies of patterned semiarid ecosystems on the Mediterranean basin and the Kalahari region have indicated that patch-size distributions of vegetation clusters follow a power-law relationship, reflecting the presence of scale-free patterns. Complementary modeling results suggested that such power laws result from the interacting effects of global-scale resource constraints (i.e., water scarcity) and short-distance processes of plant facilitation (Kefi et al. 2007, Scanlon et al. 2007). In addition, recent research by Kefi et al. (2007, 2011) indicated that the effects of increasing aridity and/or human disturbance leads to a departure from the power-law relation toward a truncated power or exponential relationships induced by the breakdown and loss of the larger vegetation patches. A major practical outcome of these findings is that the deviation of vegetation patterns from the power patch-size distribution might be used as a warning indicating that the dryland ecosystem is approaching a threshold leading inevitably to desertification (Kefi et al. 2007, 2011, Manor and Shnerb 2008*a*).

However, recent studies have found results that disagree with the previous rationale, indicating that no single scaling law of ecosystem structure emerges from the analysis of patch-size distribution of vegetation in drylands (Rietkerk and van de Kopel 2008, Maestre and Escudero 2009). In fact, modeling approaches that include both short-distance positive feedbacks (i.e., local plant facilitation) and long-distance negative feedbacks (e.g., spatial redistribution of surface runoff and plant competition for water) reproduce regular patterns of vegetation (i.e., periodic spotted or banded landscapes), which display characteristic length scales (i.e., all vegetation clusters have approximately the same size) that can be captured by patch-size distributions (Manor and Shnerb 2008*b*, von Hardenberg et al. 2010). Nevertheless, such analysis of observed patch-size distributions in real ecosystems displaying quasiperiodic vegetation patterns has not been reported in the literature. The fact that reported results for periodic ecosystems are obtained using simplified modeling approaches, together with the disparity of results from observed non-periodic dryland systems, limits considerably the use of landscape pattern analysis for the monitoring of ecosystem structure and functionality (Thompson et al. 2008). Therefore, additional empirical studies are necessary to link landscape-level metrics of vegetation patterns to ecosystem integrity (Ludwig et al. 2000, Maestre and Escudero 2009, Lin et al. 2010).

The objective of this work is to evaluate pattern fragmentation using patch-size distributions of vegetation as a measure of ecosystem integrity in semiarid landscapes showing different degree of periodicity in their spatial organization. Our assessment is based on the analysis of landscape-level vegetation patterns derived from high-resolution remote sensing in several semiarid *Acacia aneura* F. Muell. (Mulga) shrubland plots exhibiting different degrees of disturbance. Mulga landscapes are the most common woodland ecosystem in semiarid Australia, covering ~20% of continental Australia (Nix and Austin 1973). Large portions of these semiarid landscapes show patchy patterns consisting of sequences of densely vegetated "groves" and barely covered "intergroves." Mulga displays amorphous, stippled, striped, and banded vegetation patterns, and in some cases reveals a manifest periodicity (Mabbutt and Fanning 1987, Tongway and Ludwig 1990, Ludwig et al. 1999, Dunkerley 2002). The organization of these patterns is related to the concentration of water runoff and sediments from the open interpatches into the vegetated patches located immediately downslope, which improves the ecosystem efficiency for the use of limiting resources (Tongway and Ludwig 2001, Ludwig et al. 2005). Mulga landscapes provide an exceptional scenario for the study of the spatial organization of vegetation in drylands, due to their wide variety of patterns and the deep understanding of the processes that shape these spatial configurations.

Our main hypothesis is that the existence of quasiperiodic semiarid vegetation patterns breaks the suitability of power-law relations as universal descriptors for the patch-size distribution of undisturbed semiarid vegetation, and consequently, transitions from power-law relations to truncated power or exponential relationships cannot be used as unique indicators of the loss of ecosystem integrity. We specifically expect to find a clear signature of periodicity in the patch-size distribution for banded vegetation systems, when the preferential directions of the resource redistribution processes that shape these ecosystems are considered.

Materials and Methods

Study areas

This work was carried out in four study sites within two regions located on the eastern and central portions of the *Acacia aneura* range distribution in Australia: the Lake Mere site, near Louth in the state of New South Wales, and the Bond Springs, Kunoth Paddock, and Hamilton Downs sites, near Alice Springs in the Northern Territory (Fig. 1a, b). Annual precipitation and potential evapotranspiration ranges between 250 and 350 mm and between 1800 and 2200 mm, respectively (Raupach et al. 2001). Soils are massive red earths (Haplargid, sensu Soil Survey Staff 2010). Vegetation in these areas typically shows a clumped distribution with dense groves of *A. aneura* trees and perennial grasses interspaced by bare or sparsely covered open areas with physically crusted soil surface, on gentle sloping terrain (Fig. 1c). These sites are representative of

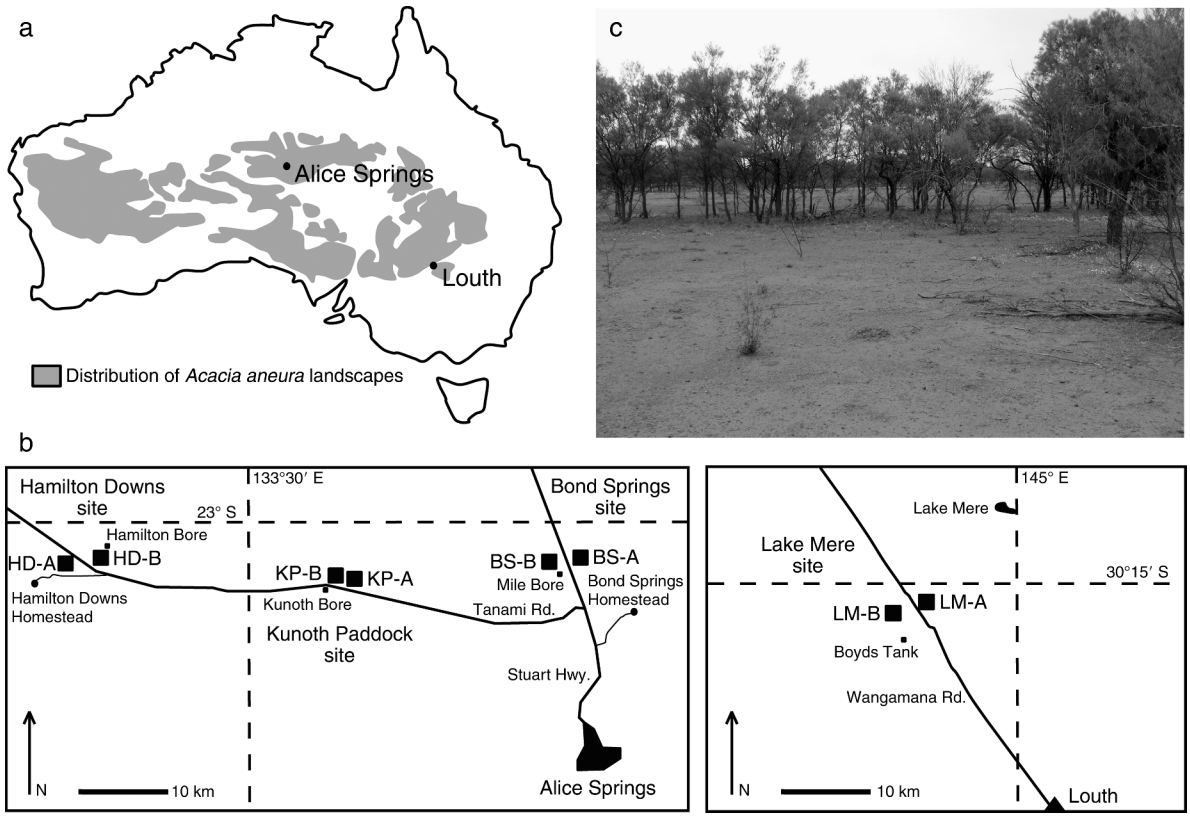

FIG. 1. Study sites: (a) regional location of the study sites (near Louth and Alice Springs) within the distribution of the semiarid *Acacia aneura* (Mulga) landscapes across Australia, (b) detailed location of the four study sites (Lake Mere, Bond Springs, Kunoth Paddock, and Hamilton Downs sites), (c) general view of a clumped Mulga landscape (Lake Mere site), where dense vegetated groves are interspaced by (almost) bare soil areas. Reference plots: Lake Mere A (LM-A), Bond Springs A (BS-A), Kunoth Paddock A (KP-A), and Hamilton Downs A (HD-A). Disturbed plots: Lake Mere B (LM-B), Bond Springs B (BS-B), Kunoth Paddock B (KP-B), and Hamilton Downs B (HD-B). *A. aneura* distribution follows Nix and Austin (1973).

Australian grazing areas, being extensively grazed by commercial livestock (mainly cattle and sheep) as well as wild populations of western grey and red kangaroos, and feral goats. Disturbance caused by grazing can be locally intense, depending on livestock management and the distance to watering points (Pickup et al. 1994). Other important disturbances that can affect the dynamics of these landscapes are wildfires and firewood collection (Berg and Dunkerley 2004).

These four study sites have been selected because they cover a variety of spatial vegetation patterns. In each study site two different plots (with areas of 1.5×1.5 km^2) were selected, one disturbed, with fragmented vegetation patterns, and the other a well-preserved landscape used as reference. The characteristics of these sites are:

The Lake Mere site is located 35 km northwest of Louth (Fig. 1b). The vegetation pattern in this site is tightly associated with the terrain landform, displaying large Mulga strands along minor dendritic drainage lines, with smaller stripes and stipples of different sizes on the interfluves. We have selected as reference plot (LM-A, Fig. 2a, Table 1), an area delimited by the former "Lake Mere" research station (Ludwig et al. 1997). Land management of this area has been regulated by sustainable grazing research programs from 1986 to the late 1990s. Further land administration has maintained the basic sustainable management principles for this area, resulting in a good landscape condition. Outside this well-preserved area, another plot (LM-B, Fig. 2b, Table 1) showing Mulga strand fragmentation was selected.

The Bond Springs site is located 25 km north of Alice Springs (Fig. 1b). Vegetation in this site is spatially organized with quasiperiodic and well-defined Mulga bands aligned along the terrain contours. We have selected as reference landscape a plot where the integrity of the banding is well preserved (BS-A, Fig. 2c, Table 1). In addition, we selected a heavily disturbed plot (BS-B, Fig. 2d, Table 1) where intense grazing, associated with the presence of a major watering point (the Mile bore) has caused an intense fragmentation of the landscape.

The Kunoth Paddock site is located 35 km northwest of Alice Springs (Fig. 1b). Similarly to the Bond Springs site, vegetation is arranged in contour-aligned Mulga bands. A well-preserved banded landscape was selected

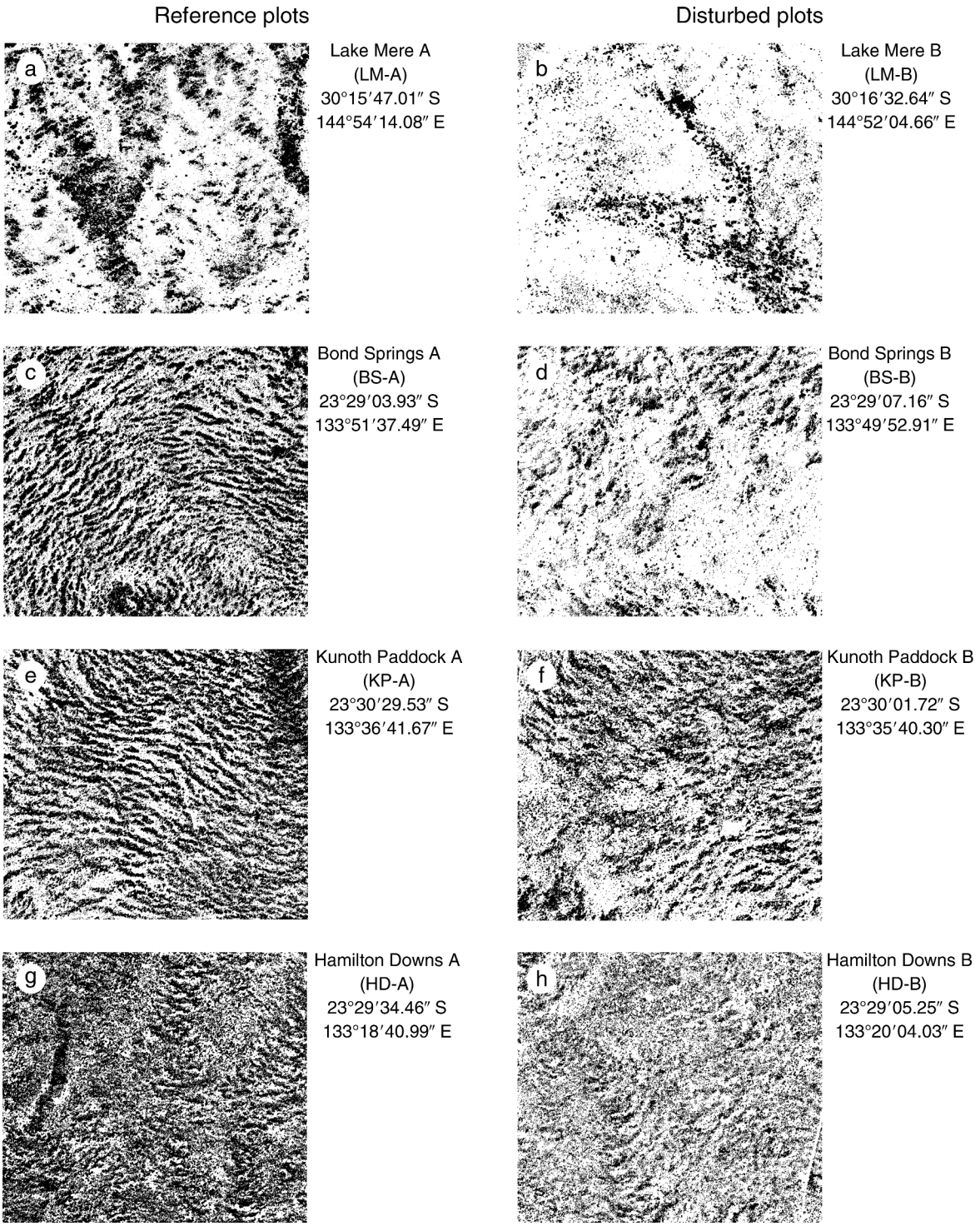

FIG. 2. Vegetation pattern (derived from remotely sensed scenes), location (center coordinates), and general characteristics of the studied *Acacia aneura* (Mulga) semiarid landscapes. Reference plots: Lake Mere A, Bond Springs A, Kunoth Paddock A, and Hamilton Downs A. Disturbed plots: Lake Mere B, Bond Springs B, Kunoth Paddock B, and Hamilton Downs B. Field view for each plot is 1.5×1.5 km^2.

TABLE 1. Characteristics of the Australian Mulga reference sites (A) and disturbed sites (B) depicted in Fig. 2.

Variable	Lake Mere		Bond Springs		Kunoth Paddock		Hamilton Downs	
	LM-A	LM-B	BS-A	BS-B	KP-A	KP-B	HD-A	HD-B
Precipitation (mm)	321	321	291	291	298	298	295	295
Elevation (m)	114–128	123–154	728–736	720–729	701–708	700–706	666–673	662–672
Mean slope gradient (°)	0.8	1.1	0.5	0.5	0.5	0.5	0.5	0.6
Soil type	red earth	red earth	red earth	red earth	red earth	red earth	red earth	red earth
Landscape status	low impacted	heavily disturbed	low impacted	heavily disturbed	low impacted	low-medium impacted	low impacted	heavily disturbed
Fractional cover (%)	28	14	47	19	48	38	55	32

as reference plot (KP-A, Fig. 2e, Table 1). A slightly disturbed plot (KP-B, Fig. 2f, Table 1) was also selected, which is located near a stocking route to the principal watering point (the Kunoth bore) and where banded patterns are still visually perceptible, though partially fragmented and less clear than in the KP-A plot.

The Hamilton Downs site is located 60 km northwest of Alice Springs (Fig. 1b). Although Mulga in this site shows some banding, the overall pattern is amorphous as observed in the nearly pristine landscape selected as reference plot (HD-A, Fig. 2g, Table 1). We have also selected a heavily disturbed area (HD-B, Fig. 2h, Table 1) described by Berg and Dunkerley (2004), where the cumulative effects of a bushfire (in September 2001), commercial firewood collection, and cattle grazing have induced a large fragmentation of the vegetation pattern.

Remote sensing data processing

The vegetation pattern analyses were derived from geo-referenced and pan-sharpened multi-spectral IKONOS (GeoEye, Herndon, Virginia, USA) and QuickBird (DigitalGlobe, Longmont, Colorado, USA) images of the study areas. Remote sensing data for the Lake Mere site were provided by a four-band pan-sharpened IKONOS scene (0.8-m pixel resolution) captured on October 2002, while data for the Bonds Springs, Kunoth Paddock, and Hamilton Downs sites were four-band pan-sharpened QuickBird scenes (0.6-m pixel resolution) captured on July 2006, August 2005, and September 2006, respectively. The high spatial resolution of these scenes (0.4–0.6 m^2 per pixel) ensures the capture of the smallest patches of vegetation and isolated Mulga shrubs within the study sites. Although the use of consistent pixel sizes is desirable for some studies due to the scale dependency of spatial patterns (Wu 2004), research by Saura (2004) indicated that image rescaling via pixel aggregation could induce spurious effects that have a larger impact on the patch-size distributions than the small effects produced by the minor range of differences in pixel size of our scenes. We therefore chose to use the original resolution of the remote-sensed scenes.

The normalized vegetation index was calculated for each remotely sensed scene. This information was used in combination with the raw spectral bands to generate binary maps of vegetation by applying supervised classification techniques (Richards and Xiuping 2006). The procedure comprised: (1) the determination of the characteristic spectral signatures for both the vegetated Mulga patches and the open interpatches in representative training areas within the scenes (10 training areas per class and remotely sensed scene, each containing at least 50 pixels), and (2) the categorization of every pixel in the images into one of the two aforementioned classes (vegetation and bare pixels) to generate binary maps, using the maximum likelihood criteria. The large difference between the spectral signatures of vegetated and bare soil areas in the scenes facilitated the classification of the images, obtaining a global accuracy of 96% (SD 1%) and a Kappa coefficient of agreement (Congalton 1991) value of 0.92 (SD 0.03), both assessed with 100 reference points per scene selected in a random scheme and interpreted manually. The four binary maps derived from the remotely sensed scenes were subsampled to obtain the two 1.5×1.5 km^2 plots described in the previous section and shown in Fig. 2. Individual vegetation patches were identified by applying a von Neumann neighborhood scheme (i.e., four immediate neighbors, no diagonals) to connect vegetated contiguous pixels (Scanlon et al. 2007).

Landscape terrain information used in this work was derived from a three-arc second (~90 m) digital elevation model (DEM) originally produced by the NASA Shuttle Radar Topographic Mission (SRTM) and subsequently processed by the Consortium for Spatial Information of the Consultative Group for International Agriculture Research (SRTM V4; CGIAR-CSI, *available online*).[4] This seamless DEM represents a significant improvement over other versions derived from the NASA SRTM data; it has undergone surface-cleaning algorithms to reduce pits and peaks, it contains no-data holes, and its accuracy has been extensively tested with field-based data and high-resolution reference DEMs (Gorokhovic and Voustianiouk 2006). The corresponding SRTM V4 tiles for the study sites were downloaded from the CGIAR-CSI interface and reprojected to Universal Transverse Mercator (WGS84 horizontal datum and EGM96 vertical datum).

[4] ⟨http://srtm.csi.cgiar.org/⟩

Vegetation patch-size distribution analyses

In addition to the analysis of patch-size distributions, we seek to identify the signature of the landscape processes that shape the spatial organization of Mulga vegetation patterns, i.e., the spatial redistribution of runoff and sediments between bare and vegetated patches that has been argued to be the main process driving the spatial organization of semiarid Mulga landscapes (Tongway and Ludwig 2001, Ludwig et al. 2005, Saco et al. 2007). Thus, the analysis of vegetation pattern must explicitly recognize the main directions of resource redistribution at the landscape level. To achieve that goal, we have adopted two approaches to obtain vegetation patch size distributions, a nondirectional and a directional approach.

Two-dimensional (2-D) patch-size distributions of vegetation were estimated without considering particular directions (nondirectional 2-D patch-size distribution analysis). In this case the size of the patches was expressed in area units (a, m^2) and all vegetation patches distributed within each 1.5×1.5 km^2 plot were considered.

One-dimensional (1-D) patch-size distributions were estimated using preferential downslope landscape directions of runoff water and sediment redistribution (directional 1-D patch-size distribution analysis). In this case the size of the patches was expressed in length units (l, m) and only vegetation patches intercepted by 20 downslope lineal transects of 500 m were considered. In order to generate these transects, we used overlapping information from the vegetation maps and the corresponding SRTM V4 data. We chose random locations within each plot as initial points to delineate the linear transects, which were then graphically outlined using the elevation information and the vegetation patterns in the downslope direction. Transect length used in this study is consistent with those used in other regional studies on Australian patchy ecosystems (Ludwig and Tongway 1995, Berg and Dunkerley 2004), and the number of transects was selected based on previous studies of vegetation patch-size distributions (Kefi et al. 2007, Maestre and Escudero 2009).

The empirical 1-D and 2-D patch-size distributions of vegetation in each plot were estimated using two different probability distribution functions, previously used in similar studies (Kefi et al. 2007, Scanlon et al. 2007, von Hardenberg et al. 2010): (1) the probability density function (PDF), which is the probability that the vegetation patches have a given area, $P(\text{Patch} = a)$ for the 2-D analysis, or a given length, $P(\text{Patch} = l)$ for the 1-D analysis; and (2) the cumulative probability distribution function (CDF), corresponding to the probability for a vegetation patch to have a size equal to or greater than a determined area, $P(\text{Patch} \geq a)$, for 2-D or length, $P(\text{Patch} \geq l)$, for 1-D.

Three different analytical models were used to describe the empirical distributions of patch sizes (S): (1) a power law, $P(S) \propto S^{-\gamma}$; (2) an exponential model, $P(S) \propto e^{-\beta S}$; and (3) a truncated power law, $P(S) \propto S^{-\gamma} e^{-S/Sc}$, where $P(S)$ is either the PDF or the CDF, γ and β are the scaling exponents (or decay rates), and Sc is the patch-size threshold above which $P(S)$ has a higher decay rate than the power law. The selection of these three models allowed for the comparison with previous work (Kefi et al. 2007, Scanlon et al. 2007, Maestre and Escudero 2009). Goodness of fit between the empirical and analytical distributions was determined using both the adjusted coefficient of determination, adj. R^2, and the Akaike Information Criterion, AIC (Akaike 1974). AIC was used to determine the analytical distribution that best fitted the empirical data.

Results

Nondirectional 2-D patch-size distribution analysis

The 2-D patch-size probability density functions (2-D PDF: probability patch $= a$) obtained for all sites best fits power-law relationships with scaling exponent γ ranging from 1.46 to 1.82, regardless of the ecosystem status (Table 2). Differences in the 2-D PDF between the well-preserved and disturbed plots are very small (Fig. 3a–d), and related to the loss of the larger vegetation patches (almost entirely for $a > 10\,000$ m^2) and minor increases in the relative distribution of the small patches (1–100 m^2), especially in the case of the Lake Mere, Bond Springs, and Hamilton Downs sites (Fig. 3a, b, d).

The cumulative 2-D patch-size probability distribution functions (2-D CDF: probability patch $\geq a$) show higher sensitivity to fragmentation of the spatial pattern. Patch-size distributions obtained for the well-preserved reference plots also show the best fit for power-law relationships in all the study sites, with scaling exponent γ between 0.70 and 0.96 (Table 2). On the other hand, the CDFs are better described by truncated power laws for the disturbed plots of the Lake Mere, Bond Springs, and Hamilton Downs sites, with lower γ values (0.53–0.62) and Sc patch-size threshold values ranging from 104 to 181 m^2 (Table 2). The only exception is for the CDF of the slightly disturbed Kunoth Paddock plot (KP-B) where the best fit is a power-law relationship with exponent $\gamma = 0.81$ (Table 2). In other words, we find in three out of the four sites (i.e., Lake Mere, Bond Springs, and Hamilton Downs) a shift from power-law distributions for undisturbed plots to truncated power-law distributions for disturbed plots (Fig. 3e, f, h). The loss of the largest patches in the disturbed plots has a marked effect on the cumulative probability distribution functions, showing faster decay rates than those of the reference power-law relationships for patch sizes larger than the threshold Sc.

Directional 1-D (downslope) patch-size distribution analysis

As shown in Table 3, unlike the 2-D PDFs for all well-preserved reference plots, the 1-D patch-size probability density functions (1-D PDF: probability patch $= l$) are

TABLE 2. Summary of scaling parameters and statistics derived for models fitted to the nondirectional two-dimensional patch-size (a = area) empirical probability distribution (probability density and cumulative probability distribution functions) of vegetation in semiarid *Acacia aneura* (Mulga) landscapes across Australia.

Site		Power-law model			Exponential model			Truncated power-law model			
		γ	Adj. R^2	ΔAIC	β	Adj. R^2	ΔAIC	γ	Sc (m^2)	Adj. R^2	ΔAIC
PDF: Probability density function; P(Patch = a)											
Lake Mere	LM-A	**1.70**	**0.99**	**0**	1.59	0.98	2649	n.a.	n.a.	n.a.	n.a.
	LM-B	**1.69**	**0.99**	**0**	1.65	0.98	1100	n.a.	n.a.	n.a.	n.a.
Bond Springs	BS-A	**1.46**	**0.99**	**0**	2.28	0.97	3483	n.a.	n.a.	n.a.	n.a.
	BS-B	**1.47**	**0.99**	**0**	2.33	0.97	2617	n.a.	n.a.	n.a.	n.a.
Kunoth Paddock	KP-A	**1.66**	**0.99**	**0**	2.64	0.98	2120	n.a.	n.a.	n.a.	n.a.
	KP-B	**1.70**	**0.99**	**0**	2.77	0.98	3303	n.a.	n.a.	n.a.	n.a.
Hamilton Downs	HD-A	**1.82**	**0.99**	**0**	3.14	0.98	2764	n.a.	n.a.	n.a.	n.a.
	HD-B	**1.71**	**0.99**	**0**	3.04	0.97	2171	n.a.	n.a.	n.a.	n.a.
CDF: Cumulative probability distribution function; P(Patch $\geq a$)											
Lake Mere	LM-A	**0.82**	**0.99**	**0**	0.34	0.81	2461	n.a.	n.a.	n.a.	n.a.
	LM-B	0.64	0.97	611	0.05	0.81	1425	**0.53**	**155**	**0.99**	**0**
Bond Springs	BS-A	**0.76**	**0.99**	**0**	0.38	0.83	3431	n.a.	n.a.	n.a.	n.a.
	BS-B	0.71	0.98	938	0.20	0.83	2533	**0.62**	**104**	**0.99**	**0**
Kunoth Paddock	KP-A	**0.96**	**0.99**	**0**	1.11	0.89	2145	n.a.	n.a.	n.a.	n.a.
	KP-B	**0.81**	**0.99**	**0**	0.77	0.78	2848	n.a.	n.a.	n.a.	n.a.
Hamilton Downs	HD-A	**0.70**	**0.99**	**0**	0.28	0.63	2357	n.a.	n.a.	n.a.	n.a.
	HD-B	0.66	0.98	1426	0.10	0.77	3755	**0.58**	**181**	**0.99**	**0**

Notes: Scaling parameters: the decay rates of the power-law and exponential models are denoted by γ and β, respectively; Sc represents the patch-size threshold above which the probability distribution has a higher decay rate than the power law. Statistics are the adjusted coefficient of determination, adj. R^2, and the difference in Akaike Information Criterion value between the lowest scoring model and each candidate model, ΔAIC. Parameters and models shown are statistically significant at the $P < 0.01$ level. Values representing the best-fitting model for each case (i.e., the model with the lowest ΔAIC value) are highlighted in bold. Abbreviations: n.a., not applicable (no truncated power-law model with a significant Sc parameter was found). Reference plots: Lake Mere A (LM-A), Bond Springs A (BS-A), Kunoth Paddock A (KP-A), and Hamilton Downs A (HD-A). Disturbed plots: Lake Mere B (LM-B), Bond Springs B (BS-B), Kunoth Paddock B (KP-B), and Hamilton Downs B (HD-B).

not always best fitted by power laws. Patch sizes for Lake Mere and the Kunoth Paddock sites (LM-A and KP-A) do display power-law type distributions, with scaling γ exponents between 1.19 and 1.29 (Table 3). However, size distributions for the reference plots of the Bond Springs and Hamilton Downs sites (BS-A and HD-A) are better described by truncated power-law relationships, with γ values around 0.82 and Sc values between 12 and 24 m (Table 3). Notably, the peaks or spikes in the PDFs of the reference BS-A and KP-A plots at characteristic scale lengths (10–20 m and 15–30 m, respectively) only emerge using this downslope directional analysis (Fig. 4b, c). Disturbed plots show, for all cases, truncated power relationships, with γ values ranging from 0.11 to 0.95 and Sc values between 2 and 11 m (Table 3). Changes in the patch-size distribution between the reference and disturbed plots are visibly related to reductions in the relative abundance or loss of the larger patches of vegetation (Fig. 4a–d).

The cumulative 1-D patch-size probability distribution functions (1-D CDF: probability patch $\geq l$) show in all cases truncated power-law relationships, although important variations are found between the disturbed and the reference plots (Fig. 4e–h). Indeed, large differences can be observed on the scaling parameters, especially for the Sc threshold size that ranges between 11 and 17 m for the reference plots, and between 3 and 9 m for the disturbed plots (Table 3). Once again, differences between reference and disturbed plots led to higher decay rates in the patch-size distribution for disturbed conditions that are associated with the decrease or disappearance of large vegetation clumps.

DISCUSSION

Scaling laws, landscape periodicity, and patch-size distributions of vegetation

Scale-free power-law type relationships of vegetation patch-size distributions have been found in a wide variety of pristine semiarid landscapes across the Mediterranean basin and the Kalahari region (Kefi et al. 2007, Scanlon et al. 2007). The occurrence of these power-law patch-size distributions has been explained as a result of local facilitation processes, and has been interpreted as an indication that a universal mechanism might rule the spatial organization of water-limited ecosystems (Sole 2007). This view has been strengthened by the renewed discussion on the critical importance of plant facilitation processes in stressful environments (Maestre et al. 2009, Butterfield et al. 2010) and by the occurrence of similar power-law relations in other ecosystems (Kefi et al. 2011). The well-preserved Mulga landscapes studied here show scale-free power-law type relationships describing both patch-size PDFs and CDFs when analyzed using the nondirectional 2-D approach (Fig. 3). These results apparently confirm the previously suggested general scaling law of spatial organization. However, our results for the directional

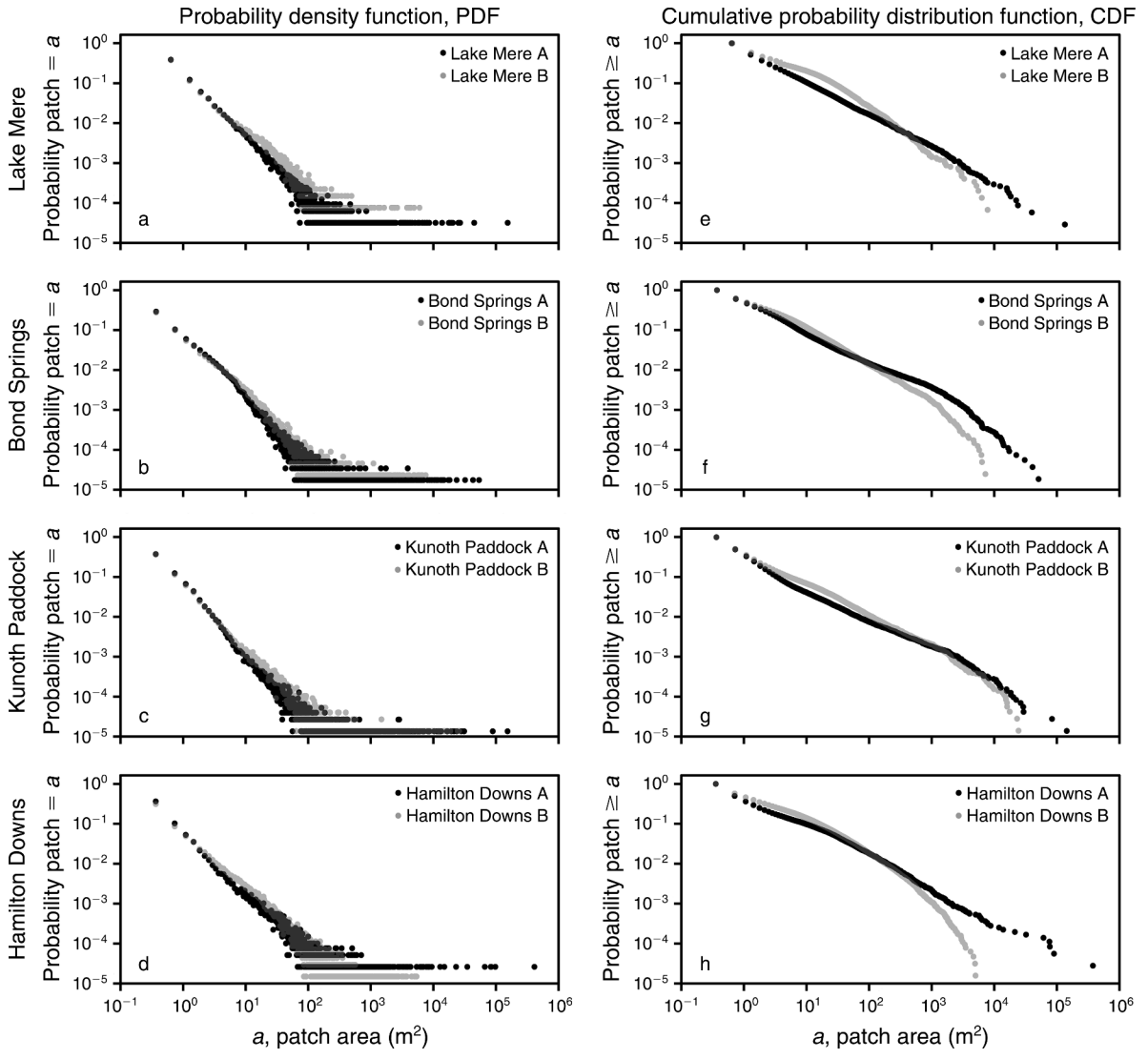

FIG. 3. Nondirectional two-dimensional patch-size distributions of vegetation in *Acacia aneura* (Mulga) semiarid landscapes. Reference plots (black dots): Lake Mere A, Bond Springs A, Kunoth Paddock A, and Hamilton Downs A. Disturbed plots (gray dots): Lake Mere B, Bond Springs B, Kunoth Paddock B, and Hamilton Downs B.

(downslope) 1-D analyses of the well-preserved landscapes show that power-law relations are inadequate to describe probability densities at some sites and cumulative distributions at all sites (Fig. 4). These results agree with those obtained by Maestre and Escudero (2009), who concluded that the patch-size distribution of semiarid vegetation is not always well characterized by power laws.

Patch-size distributions for vegetation patterns exhibiting spatial periodicities have been recently analyzed using simulated patterns obtained from models (Manor and Shnerb 2008*b*, von Hardenberg et al. 2010). These models of self-organizing dynamic vegetation patterns capture the spatial periodicity of vegetated patches as a result of short-distance positive and long-distance negative vegetation-water feedbacks (Saco et al. 2007, Rietkerk and van de Kopel 2008). Short-range feedbacks are mainly due to the positive effect of high plant density on reducing evaporation and enhancing water infiltration, which is facilitated by soil macro-fauna (e.g., creating stable, long-lived tunnels and chambers that increase infiltration capacity) and spatially strengthened by the transference of water runoff from surrounding bare areas to densely vegetated patches. In addition, the effect of long-range competition induced by runoff within vegetation clusters reduces water availability for vegetation growth at long distances and hence limits patch sizes. An important body of empirical evidence highlights the importance of these mechanisms on the spatial organization of semiarid Mulga landscapes (Tongway et al. 1989, Tongway and Ludwig 2001, Ludwig et al. 2005). These modeling studies have

TABLE 3. Summary of scaling parameters and statistics derived for models fitted to the directional one-dimensional (downslope) empirical patch-size (l = length) distribution (probability density and cumulative probability distribution functions) of vegetation in semiarid *Acacia aneura* (Mulga) landscapes.

Site		Power-law model			Exponential model			Truncated power-law model			
		γ	Adj. R^2	ΔAIC	β	Adj. R^2	ΔAIC	γ	Sc (m)	Adj. R^2	ΔAIC
PDF: Probability density function; $P(\text{Patch} = l)$											
Lake Mere	LM-A	**1.19**	**0.99**	**0**	0.66	0.95	106	n.a.	n.a.	n.a.	n.a.
	LM-B	0.97	0.95	30	0.35	0.95	36	**0.60**	**9**	**0.98**	**0**
Bond Springs	BS-A	1.04	0.98	21	0.62	0.96	54	**0.83**	**12**	**0.99**	**0**
	BS-B	0.96	0.92	69	0.48	0.98	2	**0.15**	**3**	**0.99**	**0**
Kunoth Paddock	KP-A	**1.29**	**0.99**	**0**	1.17	0.95	110	n.a.	n.a.	n.a.	n.a.
	KP-B	1.15	0.98	18	0.79	0.96	66	**0.95**	**11**	**0.99**	**0**
Hamilton Downs	HD-A	0.94	0.98	19	0.49	0.91	102	**0.81**	**24**	**0.99**	**0**
	HD-B	0.97	0.91	57	0.50	0.98	1	**0.11**	**2**	**0.99**	**0**
CDF: Cumulative probability distribution function; $P(\text{Patch} \geq l)$											
Lake Mere	LM-A	0.75	0.95	234	0.17	0.95	243	**0.45**	**16**	**0.99**	**0**
	LM-B	0.77	0.92	148	0.20	0.98	83	**0.27**	**8**	**0.99**	**0**
Bond Springs	BS-A	0.69	0.93	131	0.17	0.94	115	**0.36**	**13**	**0.99**	**0**
	BS-B	0.84	0.93	116	0.35	0.98	50	**0.28**	**5**	**0.99**	**0**
Kunoth Paddock	KP-A	0.65	0.93	121	0.13	0.92	122	**0.37**	**17**	**0.99**	**0**
	KP-B	0.79	0.95	186	0.27	0.96	175	**0.43**	**9**	**0.99**	**0**
Hamilton Downs	HD-A	0.64	0.89	267	0.14	0.98	175	**0.24**	**11**	**0.99**	**0**
	HD-B	0.92	0.91	147	0.44	0.98	43	**0.14**	**3**	**0.99**	**0**

Notes: Scaling parameters: the decay rates of the power-law and exponential models are denoted by γ and β, respectively; Sc represents the patch-size threshold above which the probability distribution has a higher decay rate than the power law. Statistics are the adjusted coefficient of determination, adj. R^2, and the difference in Akaike Information Criterion value between the lowest scoring model and each candidate model, ΔAIC. Parameters and models shown are statistically significant at the $P < 0.01$ level. Values representing the best-fitting model for each case (i.e., the model with the lowest ΔAIC value) are highlighted in bold. Abbreviations: n.a., not applicable (no truncated power-law model with a significant Sc parameter was found). Reference plots: Lake Mere A (LM-A), Bond Springs A (BS-A), Kunoth Paddock A (KP-A), and Hamilton Downs A (HD-A). Disturbed plots: Lake Mere B (LM-B), Bond Springs B (BS-B), Kunoth Paddock B (KP-B), and Hamilton Downs B (HD-B).

suggested that the existence of periodic vegetation patterns with characteristic length scales precludes the use of scale-free power laws as universal descriptors for the spatial organization of semiarid ecosystems (Manor and Shnerb 2008*b*, von Hardenberg et al. 2010). To date, however, there have been no empirical studies that either support or oppose this view, so our work provides some valuable insight.

In our case, the well-preserved banded plots in the Bond Springs and Kunoth sites (BS-A, KP-A) show clear characteristic length scales of about 10–30 m (Fig. 4 b, c), which are comparable to field-based observations of vegetation band widths (Mabbutt and Fanning 1987, Dunkerley 2002, Berg and Dunkerley 2004). The 1-D patch-size probability density functions obtained for the banded BS-A and KP-A landscapes (i.e., scale-free distributions for smaller patches with a cut-off size, and the presence of a characteristic peak, or length scale, for the larger patches) resemble the results obtained by Manor and Shnerb (2008*b*). Their modeling framework integrates the aforementioned short and long-distance vegetation-water feedbacks, within a two-dimensional isotropic space with no preferential flow direction (where flow is redistributed through an isotropic dispersive mechanism). Our results only reproduce these peaked distributions in the 1-D (downslope) analyses. This is due to the fact that vegetation patterns are influenced by factors that break the isotropy of the space and generate preferential directions on the redistribution of water runoff, as the slope of the ground surface (Lejeune et al. 1999, Valentin et al. 1999).

In the case for our Mulga banded landscapes, the main direction of resource redistribution is downslope (Tongway and Ludwig 2001) and therefore long-range competition for water between vegetation patches is predominantly in this direction. In fact, we find that the characteristic length scales in the metrics disappear when applying a 2-D analysis approach (Fig. 3b, c). We therefore suggest that the lack of long-distance negative feedbacks in the direction perpendicular to the flow is responsible for emergence of scale-free patch-size distributions in the 2-D analysis in these well-preserved Mulga landscapes. Even though all bands have approximately equal length in the flow direction, the lack of long-distance competition for resources in the direction perpendicular to the flow gives rise to a wide range of sizes (Fig. 2 for BS-A and KP-A). The 2-D pattern is then comprised by many small bands and fewer larger bands resulting in the power-law distribution that masks the periodic characteristics of the pattern, which though visually obvious, is only captured by the 1-D downslope analysis.

Effect of pattern fragmentation on patch-size distributions

Previous studies have suggested that deviations of patch-size distributions from power law to narrower truncated power-law or exponential relationships are related to fragmentation of vegetation patterns by

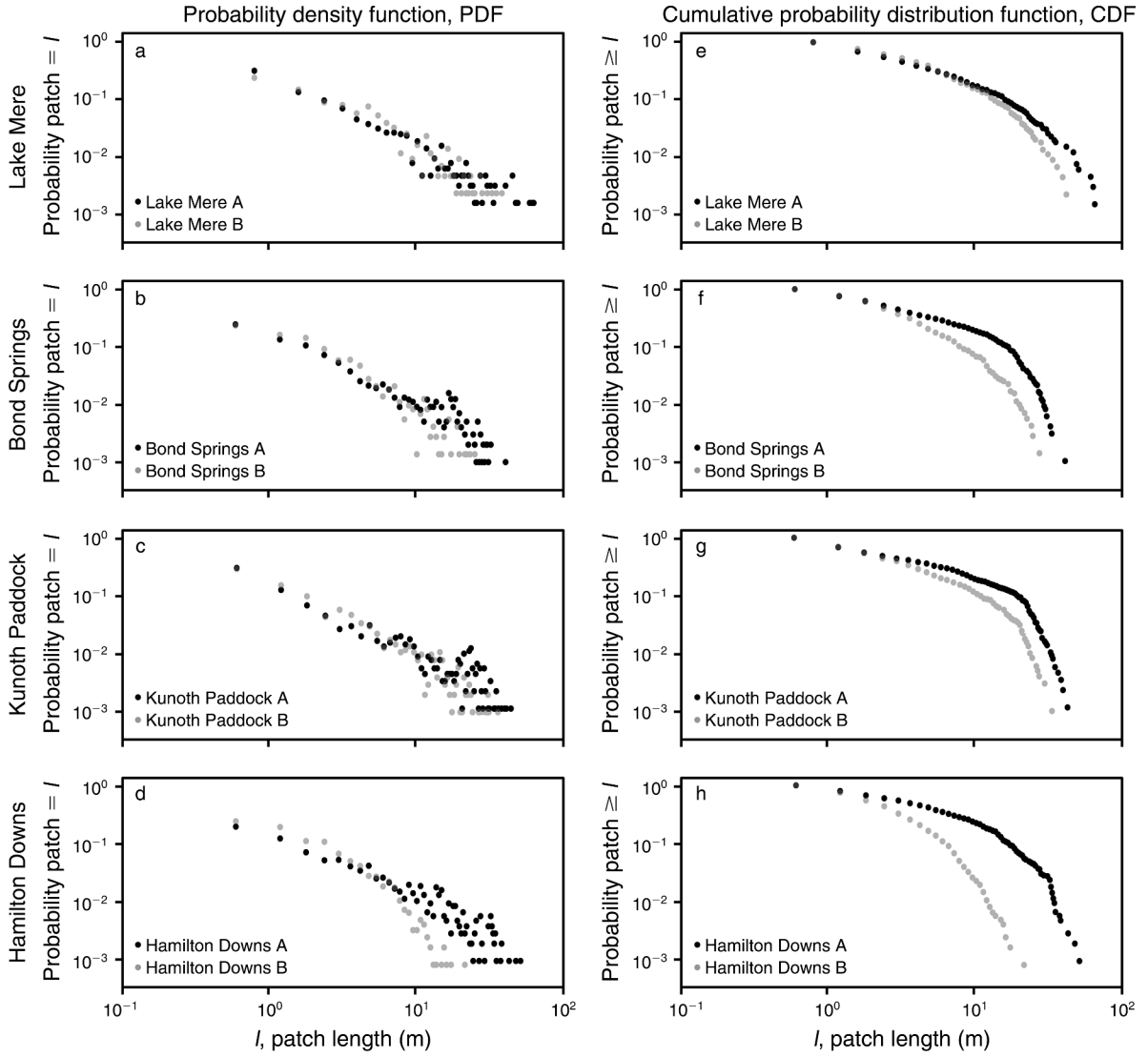

FIG. 4. Directional one-dimensional (downslope) patch-size distributions of vegetation in *Acacia aneura* (Mulga) semiarid landscapes. Reference plots (black dots): Lake Mere A, Bond Springs A, Kunoth Paddock A and Hamilton Downs A. Disturbed plots (gray dots): Lake Mere B, Bond Springs B, Kunoth Paddock B, and Hamilton Downs B.

external disturbances and could be used as warning signals for the onset of desertification (Kefi et al. 2007, 2011, Manor and Shnerb 2008*a*). Our results do not support this clear distinction. On the one hand, the two-dimensional patch-size distributions of the undisturbed plots show characteristic power-law type relationships, but we only find a transition to truncated power-law type relationships using CDFs. That is, unlike results reported by Kefi et al. (2007) for Mediterranean ecosystems under grazing pressure, in our study areas no evident changes are detected using the PDFs (Fig. 3). On the other hand, the one-dimensional patch-size distributions of the Mulga plots do not decay as power laws in most of the undisturbed plots, especially when we apply the CDF analysis (Fig. 4). The impact of fragmentation in these patch-size distributions is generally associated with reductions in threshold patch sizes Sc (Table 3), with higher decays in the abundance of the large patch sizes for disturbed conditions (Fig. 4). In agreement with the work reported by Maestre and Escudero (2009), our results suggest that deviations from power-law relations (for the patch-size distributions of vegetation) are not useful as universal indicators of the loss of ecosystem integrity and land desertification processes. We instead find that other indicators derived from the patch-size distributions of vegetation can better characterize these effects.

In general, fragmentation processes reported in this work are associated with the loss of the largest vegetation patches within the landscapes (Figs. 3 and

4). This loss also explains transitions from patch-size power-law type distributions to narrower truncated power-law distributions (Kefi et al. 2011). In fact, the preferential loss of large patches destroys any form of scale invariant (i.e., scale-free) behavior by the introduction of scale dependencies (Fig. 3 e–h). Thus, the fragmentation and loss of large vegetation patches emerges as a unifying indicator of degradation. This is not surprising because large vegetation patches are important components of semiarid ecosystems (Ludwig et al. 2000). They increase species richness while critically contributing to the regulation of the surface fluxes of runoff water and sediments, and the cycling of nutrients (Wu et al. 2000, Wilcox et al. 2003, Maestre 2004). Interestingly, the peaks or characteristic length scales that characterize the PDFs of the well-preserved banded landscapes in the Bond Springs and Kunoth Paddock sites tend to disappear in the disturbed plots (Fig. 4b, c). In these cases, the reduction in the abundance of the largest patches is also associated with the loss of periodicity depicted in the original quasi-regular landscapes.

A quick comparison between the methodologies applied here reveals that the CDF shows a higher sensitivity to pattern fragmentation than the PDF (Figs. 3 and 4, Tables 2 and 3). These findings agree with those obtained by White et al. (2008), who compared the use of both the probability density function and the cumulative probability distribution function for ecological analyses based on frequency distributions, and together suggest that CDFs are better than PDFs at capturing the impact of fragmentation in the patch-size distribution of vegetation. Despite the fact that patch-size analyses of vegetation based on the CDF have shown a reasonable ability to capture the impact of disturbances on vegetation patterns, our results suggest that lesser impacts are difficult to detect (Fig. 3g). Thus, landscape monitoring in semiarid ecosystems should also involve other approaches that are more sensitive to small changes in key landscape functions (e.g., the use and conservation of water resources and nutrient cycling), such as remote sensing or field-based landscape function analyses (Ludwig et al. 2007, Tongway and Ludwig 2011).

Implications for the study and monitoring of semiarid patterned landscapes

Our 2-D and 1-D patch-size distributions analyses for the studied semiarid Mulga landscapes show different characteristics. Differences are due to both pattern status, and to the explicit incorporation, in the 1-D analysis, of the principal direction of resource redistribution known to drive ecosystem organization. Our results emphasize the complexity of structure assessment in dryland ecosystems, and reveal the usefulness of vegetation patch-size distributions for monitoring landscape organization and pattern fragmentation.

However, the use of universal scaling generalizations for vegetation patch-size distributions of semiarid ecosystem patterns is problematic. Indeed, we find scale-free power-law type distributions in well-preserved Mulga landscapes for nondirectional 2-D analyses, but truncated power laws or peaked distributions with characteristic scale lengths when directional 1-D (downslope) analyses are applied. In addition, the shape of these distributions changes for different probability distribution descriptors (probability density function vs. cumulative probability distribution function).

Our results stress the importance of recognizing critical anisotropic landscape processes (i.e., downslope redistribution of runoff and sediments) for the detection of key ecosystem spatial properties on the patch-size distribution of vegetation such as periodicity. These distributions contrast notably with those obtained from modeling results for isotropic environments, which display very discernible characteristic length scales with sharp peaks in the patch-size distribution (Manor and Shnerb 2008*b*, von Hardenberg et al. 2010). In fact, identifying patterns unequivocally in real ecosystems is a complex task; even in the best examples of quasiperiodic landscapes (i.e., tiger bush type banded patterns), a conspicuous degree of disorder and the frequent presence of complex anisotropies make the detection of regularities very difficult (Valentin et al. 1999, Thompson et al. 2008). The directional patch-size distribution analysis approach applied in this work successfully detects the characteristic length scale of (quasi) periodic landscapes. This methodology offers a practical alternative to other approaches specifically designed for the spatial assessment of ecosystem structure, such as wavelet and spectral Fourier analysis, whose implementation for the detection of regularities could be rather involved (Barbier et al. 2006).

Our findings suggest a crucial importance of maintaining the large vegetation clumps for the preservation of the ecosystem structure and functionality in semiarid landscapes. Therefore, patch-size distribution of vegetation emerges as a valuable tool for the evaluation of ecosystem integrity, especially through the analysis of cumulative probability distributions. Land managers could benefit from the combined use of patch-size distribution analysis of vegetation and other indicators of landscape functionality, as diagnostic tools for monitoring semiarid ecosystems.

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